THE HABITS OF FISHES.[1]

By REVERE RANDOLPH GURLEY, M. D.

Sometime Fellow in Clark University.

INTRODUCTION.

In reading Darwin's *Expression of Emotions* one becomes impressed with the idea that while for the special purpose to which that work relates, it suffices to say that certain movements are the direct outcome of the constitution of the nervous system, for the broader purposes of evolutional neurology the real question is: How did the nervous system come to be such as it is; that is, how has it come about that there has been developed just that series of nerve mechanisms which corresponds to the demands made upon the organism by its environment? It is not enough to say that it has arisen through natural selection unless we can, without violating scientific probability, show in some precise and detailed way how the necessary gradations could have arisen and been selected. Instead of looking around for a god-send in the way of "spontaneous" variations we would, as Eimer insists, better look to physiological laws for the basis materials upon which natural selection can work. To this end the tracing of the steps by which, in the fishes, from a comparatively simple instinct, a comparatively complex instinct with various accessory instincts, has arisen, cannot be without value; for it shows how a progressive change of conditions in the environment has originated a definite correlative change of function in the organism. And the paucity of cases in which such a definite correlation is demonstrable, renders every one valuable.

In the study of animal psychology one method especially offers a chance which should not be neglected, namely the comparative method. Careful observation and comparison from species to species of a genus, from genus to genus of a family, and from area to area (geographical distribution), may be ex-

[1]This paper embodies conclusions formed in part during five years of work in the U. S. Fish Commission, and in part as the result of a collection and comparison of all data upon the habits of fishes in the first two Reports of the Commission, made while at Clark University. I here extend thanks to Prof. B. Warren Evermann and Dr. Fritz Schwyzer for their kindness in criticising manuscript, and to Dr. W. C. Kendall for furnishing data.

pected to give some clue to relative antiquity of instincts; the oldest instincts, like the oldest structures, being (in general and subject to more or less qualification) those in which the most species of a genus, genera of a family, etc., agree; and the most recent being those in which the species, genera, etc., differ the most.[1] The present method of studying the psychic development of the young is, of course, excellent. But just as comparative anatomy preceded embryology, so here, as a preliminary, the comparative may prove more profitable than the developmental psycho-physiology.

For the evolutional physiologist the most important task is the locating of the cardinal points of the spiral life curve, that is, the division of the life cycle into its separate terms, the analysis of their interdependence, and the determination of their order of sequence *and the conditions which determine that order.* In the fishes the determination of these cardinal points is, fortunately, not difficult. They here mark the periodically recurring instincts of migration and reproduction. And just as we find Ryder[2] implying that repetition of structure is conditioned upon repetition in embryonic environment, so here we can assert that cyclical recurrence of instinct is the outcome of cyclical recurrence of environmental stimuli.

Considering that on account of their economic importance, we have a fuller and more accurate knowledge of the habits of fishes than of those of other animals, it is surprising that up to the present there has been no attempt at a connected and systematic presentation. Except for a few paragraphs in Darwin and a few pages in Romanes, there is practically no literature apart from numerous scatterd notes, mostly in the Reports of the various Fish Commissions and Fish Cultural Societies. The present paper is merely an attempt to bring order out of chaos.

The conclusions arrived at are: (1) the significant fact in the temperature relations of fishes is the distribution of spawning with reference to the signs of the temperature zodiac; (2) the cause of spawning is the definite temperature trend in *one* direction; (3) structurally similar forms tend strongly to sustain in their spawning similar relations to the temperature curve; (4) in at least some cases apparent exceptions can be harmonized with the law; (5) for a given species the temperature relations which determine its migration and probably also its geographical distribution, are the same as those which determine its spawning; (6) these facts demonstrate the presence of a temperature responsive nerve mechanism; (7) this mechanism is a character

[1] No one will suppose that this is regarded as a new method. In Comparative Psychology, however, it has not been utilized to any extent.

[2] Woods Holl Lectures for 1894, 1895, pp. 23-55.

of prime importance and is entitled to at least super-Family rank; (8) the existence of this mechanism explains *why* with in-cooling spawning[1] is, and *must be*, associated to-cooler[1] migration and boreal distribution, and with in-warming spawning, to-warmer migration and austral distribution; (9) by a working backwards from the time of most successful hatching, the time of spawning has been determined via natural selection; and (10) the time of spawning being so fixed, by a further working backward, natural selection has determined the time of precedent migration.

Spawning Habits.

1. *The significant fact in the temperature relations of fishes is the distribution of spawning with reference to the signs of the temperature zodiac.*

As to the temperature relations of spawning, it must first be noted that it is nearly all concentrated into two fairly distinct periods, a fall period from about September 1 to freezing (November), and a spring period from thawing (March) to about July 1. It is not contended that these limits are exact. Some fall spawning begins late in August, or even a little earlier in high latitudes and altitudes, and a somewhat larger amount lasts into December, but this is merely delayed fall spawning. The very purpose of this paper, however, is to insist upon the fact that the determinant is *not* the calendar, but a given temperature *taken in connection with the direction of temperature trend.* Mere contact with water of a given temperature cannot alone be the cause of spawning, for in the nature of things such contact occurs twice every year, once on warming water and once on cooling water, while spawning occurs but once. Though perhaps not entirely new, this relation needs to be emphasized and may be thus formulated: *As regards spawning, fresh water (and probably all other) fishes fall into two groups, those which spawn in warming water and those which spawn in cooling water.*

2. *The cause*[2] *of spawning is the definite temperature trend in* one *direction.*

With marine fishes our knowledge is least certain for those species which, like the cod, spawn eggs which rise to the surface ("floating" eggs). But everything we do know tends to show that with them, too, water temperature is the cause of spawning; for they spawn within fairly close time limits, and spawning is retarded or advanced by unusual fluctuations of temperature from the average, just as is the case with the beach

[1] In-cooling spawning: Spawning in cooling water. To-cooler migraing: Migrating from warmer water to cooler.

[2] Or, better, the environmental factor, the immediate stimulus.

spawners and the anadromes,[1] where our knowledge is more complete.

The rule certainly holds for the ocean bottom spawners. Thus, to take a single instance, the movements of the Norwegian herring (which spawns in warming water) to its spawning grounds depend on temperature, most being caught on the spawning beds between 12 and 14° C., cold weather diminishes the yield of the fisheries, the higher the temperature the deeper the spawning grounds, and the Dutch fishermen set their nets by the thermometer.

With both beach spawners and anadromes, in the case of those species ripening in warming water, spawning takes place in a regular progression from south to north. Occasional accordant exceptions occur. For an actual example, an in-warming-spawning species is known to spawn earlier in the northern of two closely approximated streams that stream being from local causes the warmer. Further, the regular progression across the parallels of latitude finds its counterpart in an equally regular progression with increasing altitude. Moreover, spawning takes place earlier in warm seasons, and later in cold ones. With shad the proportion of ripe females taken early in the season, to the whole number of ripe females caught, is greater in warm seasons, and then ripe females are scarcer later in the season. The exact reverse holds for those species which ripen in cooling water, an equally regular progression occurring from north to south and from high altitudes to low. In cold seasons spawning takes place earlier, in warm seasons later, and it occurs earlier in the colder of two otherwise similar and closely approximated streams. Finally, there is actually observed with both classes of fish, a thorough correspondence, increment for increment, between progressive approximation in water temperature to the spawning point, and progressive approximation in the reproductive organs to full ripeness.

3. *Structurally similar forms tend strongly to sustain similar relations to the temperature curve, that is, to spawn either all on its ascending or all on its descending limb.*

This subject cannot be here treated in extenso but it may be mentioned that all the minnows (Cyprinidæ), the catfishes (Siluridae), and the sunfishes (Centrarchidæ), spawn in warming water, while among fishes spawning in cooling water are all the cods (Gadidæ), and also probably all the Salmonids. The last will now receive more extended discussion. The following is a list of the native American species with their spawning times:

---

[1] Anadromes: Fish ascending rivers annually to spawn.

		In cooling water.	In warming water.
Whitefishes (*Coregonus*); 8 species,	Late fall	x	
Atlantic Salmon (*Salmo salar*),	" "	x	
Sebago Lake Trout (*Salmo salar sebago*),	" "	x	
Columbia River Trout (*Salmo mykiss Clarkii*),	Spring		?
Yellowstone or Cut-Throat Trout (*Salmo mykiss Lewisi*),	"		?
Utah Lake Trout (*Salmo mykiss virginalis*),	"		?
Steelhead (*Salmo Gairdneri*),	Feb.-May		?
Rainbow Trout (*Salmo irideus*),	Nov.-May [1]	x	
Brook or Speckled Trout (*Salvelinus fontinalis*),	Late fall	x	
Greenland Charr (*Salvelinus alpinus stagnalis*),	" "	x	
Dolly Varden Trout (*Salvelinus Parkii*),	" "	x	
Chinook (or Quinnat) Salmon (*Oncorhynchus tschawytscha*),	July-Dec,[2]	x	
Blueback Salmon (*Oncorhynchus nerka*),	Aug.-Nov.	x	
Humpback Salmon (*Oncorhynchus gorbuscha*),	Aug.	x	
Dog Salmon (*Oncorhynchus keta*),	Sept. or somewhat earlier	x	
Silver Salmon (*Oncorhynchus kisutch*),	Late fall, early winter	x	
Great Lake Trout (*Cristivomer namaycush*),	Sept.-Dec.	x	
Grayling (*Thymallus signifer*),	April		?

From this list it appears that as a whole the Salmonids are fall spawners, that is unquestionably spawners in cooling water; but a few species are aberrant in this respect and this brings us to our next consideration.

4. *In at least some cases apparent exceptions can be harmonized with the law.*

Before taking up this proposition, however, one current but erroneous idea must be corrected. In so far as it has been alluded to at all, it seems to have been tacitly assumed that spring spawning *must* mean spawning in warm water. So unquestioningly has this been assumed that there are few thermometric data to which to appeal. It is, however, demonstrable

---

[1] See below.

[2] July only in high altitudes.

that at least it may be, and it is quite probable that in some cases it is, associated (via a temperature induced migration) with the exact opposite, viz., spawning in cooling water. As examples of the latter may be cited passage from the bottom water of a lake at maximum density temperature (4° C.) into tributaries just thawing (that is, approximating to 0° C.), and passage a little later in the season from a warming lake or ocean into snow fed streams. The assumption that spring spawning *necessarily* means spawning in warming water, is then entirely unwarranted.

Now for the explanation of the aberrancies. The American Salmonids which exhibit the anomaly of spring spawning are:

Salmo mykiss (3 varieties).
Salmo Gairdneri.
Salmo irideus.

First, as regards the interrelation of the species. Jordan and Evermann think *Salmo Gairdneri* nothing but *S. irideus* which has descended to sea and returned, and Gilbert and Evermann know no way of distinguishing the young of the two species. Whence it is at least possible that the three exceptions are in reality but two.[1] Second, in all these forms the spring spawning either ensues upon migration into, or takes place in mountain (and mostly, if not entirely, ice-fed) streams which, as has been shown, do not necessarily warm with the advancing season, the ice or snow only melting the faster. Third, in the case of *S. irideus* we are not confined to presumptions. In the McCloud River, California, it spawns from January 1 to May, but that this is *not* spawning on warming water is shown conclusively by the fact that when brought from the McCloud to the Wytheville, Virginia, hatchery, it shifted its spawning time *not forward to spring but backward to fall*, and spawned from November to March. The inferences are that at Wytheville a temperature is reached in November which is not reached in the McCloud until January, and that the McCloud is about the southernmost point in the distribution of the species, because farther south the temperature in winter does not sink to the spawning point. The large salmon of the Danube (*Hucho hucho*) runs up the tributaries of that river from March to May to spawn. In the absence of data and considering the similar migration, it is not unreasonable to suppose that this species, and also the graylings which spawn under similar conditions of migration, may conform to the rule.

[1] The case stood thus when the above was written in 1895. In the latest authoritative pronouncement (Jordan & Evermann, 1896, Bull. U. S. Nat. Mus., XLVII, pp. 488-500) all three species are recognized, but apparently as foci around which a number of variations group themselves, and intermediate varieties are referred to.

5. *For a given species the temperature relations which determine its migration, and perhaps also its geographical distribution, are the same as those which determine its spawning.*

Under Migration Habits it will be shown that those species which are stimulated to spawn by warming water are equally stimulated to migrate by warming water, and *vice versa* for forms stimulated to spawn by cooling water, subject only for the Salmonids, to the (probably only apparent) exceptions already discussed. It remains here only to point out that those forms which spawn in warming water are all austral forms, whereas those which spawn in cooling water are all boreal forms. Both of these classes meet in the temperate zone, but it seems a fair inference that their range, northward in the one case and southward in the other, is checked at the limits where their respective spawning temperatures disappear; that is, the austral forms cannot range farther north than the place at which the highest summer water temperature reaches the spawning point, or the boreal forms farther south than the place where, at the lowest winter temperature, the water cools to their spawning point. At least the high altitudes which mark the southernmost limits of the ranges of the rainbow and the Yellowstone trouts, speak for this view.

6. *These facts demonstrate the presence of a temperature-responsive nerve mechanism.*

The word "demonstrate" is used advisedly, for it would be literally inconceivable (that is, opposed to all biological analogy whatever) that such a progressive development of the reproductive organs, extending over months, should be independent of nervous control. Any objection based on the lack of actual anatomical demonstration of the mechanism, would prove equally well that the mammary development of pregnacy is independent of nervous control. Consisting of more than one neurone (a nerve cell plus its fiber), the utero-mammary reflex arc cannot be demonstrated anatomically, that is, by the usual degeneration methods. Still its existence *must* be conceded throughout the whole mammalian class; and as it is not known outside that class, it becomes just as important a taxonomic feature as the uterus or mammæ, for, like them, it persists over equally wide groups, areas and times. As biological philosophers, therefore, it behooves us to remember that besides the convenient, naked eye anatomical characters utilized for classification, a number of physiological characters exist which are perhaps less immediately evident, but which are none the less real and important.

7. *This mechanism is a character of prime importance and is entitled to at least super-Family rank,*

For it plays the dominant roll in the fish's life. Just as much

as, if not indeed more than, the Salmonidæ are fishes with abdominal ventral fins, two dorsal fins (an anterior rayed, a posterior adipose), scaly bodies without barbels or spines, with distinct maxillaries, naked head, ctenoid scales and siphonal stomach with many pyloric cæca, are they fishes which (on the whole and small fluctuations in the life cycle perhaps apart,) *tend to seek cooler water.* Indeed, this is their fundamental dynamic character, the character which is back of their migrations and habitats, which latter have, in turn, developed their generic and specific differences. In every element by which we rate the taxonomic value of biologic characters, namely persistence over wide groups, areas and times, this nerve mechanism (demonstrated by its effects) must be accorded high biologic rank. For though the Salmonids have been able to change almost everything else (habitat, mode of life, feeding habits, etc.) and coincidently have varied through species and genera into families, there is not at present a proved instance of any species having varied to spawning in warming water. Indeed there would seem good reason for believing that they could not possibly so vary, for a change by an abrupt shift-over would manifestly be impossible, and slow variations toward such a change could only consist in a shifting of the spawning time toward a warming water season, a shifting which, as shown on p. 416, would necessarily be eliminated through natural selection.

It must be accorded at least super-Family rank inasmuch as both the Argentinidæ (capelin and smelt family), and the Salmonidæ (salmon family proper) in all its genera and species as far as at present known, agree in possessing it. That is, it antedates their divergence and, if the considerations urged on p. 420 have any force, it certainly antedates the present streams, since when the anadromous Salmonids were beach spawners it already dominated their to-beach migrations.

8. *The existence of this mechanism explains* why *with in-cooling spawning is*, and must be, *associated to-cooler migration and boreal distribution*, and with in-warming spawning, to-warmer migration and austral distribution.

No species could be at once in-cooling spawning and to-warmer migrating, because it would constantly migrate away from the only waters capable of developing the reproductive organs. Further, were such a combination possible, we should find at least some in-cooling spawning species with an austral distribution, but we do not. When, however, we once admit the necessity of the co-existence of in-cooling spawning with to-cooler migration, as two phases of action of the same nerve mechanism, we at once see *why* in-cooling spawning and to-cooler migrating species must have boreal distribution. For they will constantly be fended off from the warmer southern waters both

by repulsion of contact and by the inability of finding there water cool enough to develop the reproductive organs. *Mutatis mutandis*, we have a similar explanation for the actual association of in-warming spawning with to-warmer migration and austral distribution.

If it is urged that *a priori* we might conceive of cyclical variations (between, merely by way of example, a summer to-warming and a winter to-cooling impulse or, *vice versa*) it can only be said that though the possibility is not to be denied, no such actual case is known.

9. *By a working backward from the time of most successful hatching, the time of spawning has been determined via natural selection.*

Though the conditions are such that general reasoning can hardly be gainsaid, probably the best proof of this principle is the following actual case. In the early days of fish culture Mr. N. W. Clark hatched whitefish eggs in spring water at 47° F. with the result that hatching took place too early, all attempts at artificial feeding failed, and the fry starved to death. Next year he used the same spring water, merely interposing a cooling ice pond, and 50% were successfully hatched, beginning about April 1.

The whole subject being epitomized in this case excessive elaboration of argument is unnecessary. The fry must not hatch too early or they will starve, their food not hatching out until about March or April. If they must not hatch too early the eggs must not be deposited too early, and those fish which spawn too early will leave no descendants to perpetuate their over-readiness.

Equally they must not be deposited too late. Here, however, the environmental conditions are not so exacting, and accordingly we find that with most of the late fall spawners the end of the spawning season is not so sharply defined and tends to fray out into the winter. At the beginning of the season the water is comparatively warm and each day involves a disproportionate amount of development, but as temperature lowers each day possesses a constantly decreasing incubation value.[1] A few days too late, therefore, has no such potent effect as a few days too early. Besides, a delay of a week at 33-35° F. in spawning will be made up rather quickly as the water warms in spring, every day then doing as much as several in winter.

---

[1] The rule of 50 days at 50° F. and 5 days more or less for every degree lower or higher, holds fairly well for many of the Salmonids. Attention is directed to the very great variation in time for a small variation in temperature. Thus compare 50 with 45 and 35. At 50 each day represents 1/50 of the development, while at 45 it represents only 1/75, and at 35 only 1/125 of the whole development.

That this reasoning is correct may be inferred from the comparatively few cases of fall spawners whose eggs hatch before winter. With the Chinook Salmon, for example, the limit of the end of the season is almost as sharp as the beginning. Unlike the later spawners which, stimulated to spawn when a certain point is reached, continue to be stimulated for a number of degrees below (that is, the stimulus does not press simultaneously and with irresistible force on all individuals alike), the vast majority of the Chinook Salmon spawn within a short time (about two weeks, at any one place). And why? Because their eggs hatch in about 35 days and the fry must be out and sufficiently developed in time to seek winter quarters.

It is not to be supposed, however, that delay in deposition beyond somewhat narrow limits, is an indifferent matter. Eggs that do not hatch about the time of thawing produce fry belated in the race and which stand a greatly increased chance of destruction, for at this period a week's delay is serious. Every day hosts of hungry enemies ready to seize them in the egg, are arousing from their winter's sleep, and even after hatching the critical period of egg sac absorption, when the fry are feeble and hampered in their movements by the bulky sac, must be passed through in the face of the enemy. So that it is certain there is some limit and that here, too, natural selection has set its seal.

With the spring spawners natural selection has also operated but in a different way. The most characteristic difference between the spring spawners as a class and the fall spawners as a class, is the rapidity of incubation in the former. In part this is, of course, attributable to the higher water temperature, but the disparity is sufficient to indicate that natural selection has come into play. For example, shad eggs require only from 10 down to 4 or even 3 days for incubation, according to the temperature.

In the late fall and through the winter the sandy-gravelly beaches and shallows are deserted, for at the advent of ice they are abandoned by the spawn eating fishes which take refuge in the warmer depths. It is at this period that most beach spawning occurs. Here the eggs lie in comparative safety through the four months required for their development in the icy waters. But in spring on the open beach, eggs are very much exposed to enemies, to fungus and to asphyxiation by mud. Consequently, other things being equal, those eggs will succeed best which are held back (that is, the spawners of which are not stimulated to spawn) until the temperature has risen to such a point as to minimize the time of exposure on the beach. These considerations are reinforced by the known facts that the fry have somewhat narrow temperature limits of maximum

vigor. Thus, lethargic below 65°, shad fry thrive between 68° and 72°. En route to Germany they weakened very fast at 73° and all died in four days.[1] On transcontinental journeys 62-75° was tolerated, and 80° was the danger point. Thus, there must be some upper temperature limit beyond which extinction lies. Whence, among a number of eggs deposited over a somewhat protracted period, those will hatch best and the fry from them will thrive best which were spawned at the right time for the average season. The only way by which such an arrangement could be affected is by the selection of individuals varying favorably with respect to a thermal reflex arc.

10. *The spawning time being so fixed, by a further working backward the time of precedent migration has likewise been determined by natural selection.*

For if they are to spawn at a certain place at a certain time they must leave in time to reach it. We may naturally expect that they must start within fairly narrow time limits, for while laggards will leave no progeny to perpetuate their unreadiness, on the other hand they cannot start too early because, for many species at least, their stay in fresh water leads to death from exhaustion, the outcome of abstinence from food, injuries and attacks of fungus (*Saprolegnia*), immediately after spawning, Their stay in fresh water, therefore, while it must be long enough for spawning, cannot be much lengthened with impunity, or death would precede spawning, thereby bringing about the elimination of the over-ready.

Migration Habits.

Although we are not here directly concerned with the origin of the seek-the-beach impulse, that impulse being taken as our point of departure, it may be pointed out, parenthetically, that it is as certainly temperature-induced as its derivative, the anadromous habit; for the evidence is of the same kind and amount in the one case as in the other, the to-beach migrations taking place in a regular succession from parallel to parallel, northward in the case of species migrating on warming water, and southward in the opposite case. Indeed, so regular is this succession that along-shore migration was formerly believed in.

We now come to the consideration of the anadromous, or river ascending habit. Facts will be adduced to prove that this habit is merely an extension and further elaboration of the seek-the-beach impulse. The foregoing contentions being admitted, the requirements of a sound hypothesis will be satisfied if it can be shown that: A, there are *de facto* beach spawners; B, in type of egg the beach spawners agree with the fresh water species,

[1] Probably here other factors (lack of change of water) co-operated.

and differ from the pelagic forms, and that this difference suffices to explain (a) why species of pelagic genera are so rare in fresh water, and (b) why beach spawners are now so uncommon; C, having once attained to a seek-the-beach impulse, the conditions on the beach were such that, natural selection not opposing, the beach spawners must, through the mere continued action of the temperature responsive mechanism, be led, step by step, into the forming streams of a rising continent; and D, in the streams the necessary accessory habits have been evolved, all in accordance with accepted biological principles.

A. *There are de facto beach spawners.*

On the English coast at least eight species are known which it is unnecessary to enumerate.[1] More important, as being nearly related to the Salmonidæ, is the surf-spawning capelin (*Mallotus villosus*). The herring (*Clupea harengus*) is another species spawning above the ooze area.

B. *In character of egg the beach spawners agree with the fresh water species, and differ from the pelagic forms, and this difference suffices to explain: (a) why species of pelagic genera are so rare in fresh water, and (b) why beach spawners are now so uncommon.*

The eggs of the true fishes (Teleosts) are mainly of two classes, sinking eggs and floating eggs. In either class the eggs may be separable or adhesive.[2] The sinking egg and the adhesive floating egg occur on the beach and in the streams. The free floating egg, however, never occurs in fresh water. Indeed, it could not possibly occur there, as experience in the artificial hatching of these eggs has abundantly demonstrated that the slightest sediment is fatal to them (causing them to sink and those that sink are inevitably lost), and further, that motion is equally fatal, rupturing their delicate shells. Here, therefore, we find a sufficient reason why all marine forms have not become anadromes. Besides it was not necessary that they should, for natural selection has operated to preserve them in an entirely different way, namely by a vast increase in fertility and by throwing over their eggs the Perseus cap of transparency.

If these considerations are correct, it is easy to see why beach spawners are now comparatively uncommon. For on account of their egg type they have always been potential anadromes, and, for reasons given below, the mere continued action of the seek-the-beach impulse must have tended to impel them into the forming streams. That the egg type is the determinant factor in the matter is further implied by the fact that the only

[1] McIntosh: Bull. U. S. Fish Com. for 1893 (1894), XIII, pp. 241-44.

[2] For purposes of fish culture adhesiveness is so important a quality that eggs possessing it are grouped into a separate class.

fresh water species of the pelagic cod family, namely *Lota lota*, has simultaneously with its deviation from the ancestral habitat, deviated from the ancestral to a fresh water type of egg (sinking egg of large size as against the minute floating eggs of its pelagic congeners).

C. *Having once attained to a seek-the-beach impulse the conditions on the beach were such that, natural selection not opposing, the beach spawners must, through the mere continued action of the temperature responsive mechanism, be led, step by step, into the forming streams of a rising continent.*

For if, as urged, that impulse is induced by temperature stimulation of a reflex arc, then on a rising continent with its gradually forming streams, there must occur just that further elaboration of the seek-the-beach impulse that we now see in the anadromous instinct, provided only that natural selection does not oppose. For with a progressively chilling atmosphere, the coolest water will be found where the proportion of water surface and water movement to water bulk is greatest, as in shallow bays, and *de facto* the capelin spawns in the surf. But the coolest of all will be found in estuaries, for here it comes from the streams where the proportion of surface and movement to bulk is ad maximum. Wherefore, to-cooler migrating species advancing to the beach will be deflected more into the estuaries and most into the streams. Up these they will, in accordance with the ever acting physiological impulse of seek-the-cooler, gradually progress, for with the lengthening of the streams the coolest water will ever be found at the receding headwaters.

And, parenthetically, what has been shown here for to-cooler migrating and in-cooling spawning forms, applies equally well, *mutatis mutandis*, to to-warmer migrating and in-warming spawning species. They will find warmer water in the estuaries, and the warmest of all in the streams.

The determinant of the salmons into the rivers would thus appear to be difference of temperature. What actual evidence is there for this view? Jordan[1] says the blue-back and hump-back salmons ascend only snow fed streams having sufficient volume to send their waters well out to sea. Contact with cold water probably brings them up earlier than would otherwise have occurred. Spring freshets mean heavy spring runs and correspondingly lighter fall runs. Evermann thinks fresh water, and possibly water of a colder temperature, is the determining factor (letter). And Armistead says that though it has been stated that "fish"[2] pass from the sea into the rivers be-

---

[1] Science Sketches, 1888, pp. 51-52.

[2] Bull. U. S. Fish Com. for 1893 (1894), XIII, pp. 93-99. "Fish" is a very loose statement, as everything turns on the species. But it will be noted that he mentions "salmon."

cause the latter are warmer, he has found the sea, at least in some places, in late spring often a great deal (very often 10° or more) warmer than the rivers. When in early spring sea temperature is low, no such large runs occur in the Solway as later. In March with east winds, salmon do not run nearly so well as in April, or in April as in May. At Douglas Hall, though fishing was legal from February, the spring run was so regular that nets were not set (scarcity making it unremunerative) before the end of March and some not before April. But later, as the sea warms, a good many run. If it remains cold and the sea temperature low, none run, but as soon as the condition reverses, in come the fish.

Now while, as has been shown, in general river temperatures fluctuate more rapidly than sea temperatures, this does not necessarily apply to streams which flood in spring from the melting of ice and snow. On the contrary many and (though length and volume would make each case different) probably most of such streams retain a low temperature for weeks, in fact till the complete melting of the ice supply. These facts are, moreover, perfectly consonant with the fact that in general the runs of the Salmonids of our west coast take place in the spring progressively from south to north, for the sea warms and the ice melts progressively from south to north, both factors cooperating to make the rivers relatively colder. Further, it agrees with the fact that the runs occur earlier in warm seasons and on freshets. This view accords well with the fact that the blue back and chinook salmons run in both spring and fall, for twice the rivers must be a given number of degrees colder than the sea, while it also affords an explanation of the fact that the dog, humpback and silver salmons do not run till fall, for these last three species are probably out of reach of the rivers. Thus when they come in from sea (which the dog salmon is definitely known to do) they are probably too late to strike cold river currents, the rivers having by that time approximated to or overstepped the sea temperature.

D. *In the streams the necessary accessory instincts have been evolved, all in accordance with accepted biological principles.*

The older fish culturists and some ichthyologists held the view, often in a rather extreme form, that the anadromes were guided by an unerring instinct back to the place of their origin, and such statements were current as that a fish might be depended upon to return not only to the same river in which it was hatched, but to the same tributary of that river, and again, that a fish hatched below a dam would have no instinct to go higher than that dam, wherefore if it were desired that the young on their return from sea should go higher, the eggs must

be hatched higher up, etc. Jordan[1] has, fortunately, exploded this myth, and given a rational and credible explanation which does not deify instinct and make of it a fetich. Briefly, he says fish do not always go up the same river and when they do it is because not ranging far off shore, the chances are large that it will be the current of *that* river they will encounter first when moving inshore. As a defunct hypothesis, therefore, the older view will require no further notice.

The principal accessory instincts which have become superadded in the anadromes as a result of stream life are: *a*, abstinence from food; *b*, head-to-current impulse; and *c*, choice of spawning grounds.

a. *Abstinence from food.*

This habit has many degrees and probably is strict in direct ratio to the length of time required ad minimum and the amount of time available ad maximum, for the species to reach the spawning grounds. We may imagine that when the streams were short the fish could feed by the way and still reach the spawning grounds in time. Even this view, however, might have to be qualified, as only a short stay in fresh water is detrimental to some species from their susceptibility to disease, principally attacks of fungus. Still, in general the food-refusing habit is strict in proportion to length of travel, though this has exceptions, and it may be that in some cases absorption of impulse in the reproductive and motor systems, may suffice to explain the phenomena. It is, however, clear that there must be *some* length of migration which will require the fish to push on under penalty of being belated and leaving no progeny to transmit their hungriness and tardiness at the finish. Given, then, the ever lengthening streams of a rising continent, each year the journey is longer, and less time can be given to feeding by the way. Natural selection would then gradually weed out those individuals which had the feeding impulse strong, and favor those which tended to concentrate their feeding and motor-sexual functions into different portions of the yearly cycle. This is exactly what occurs with those salmons which return to sea after spawning, for they begin feeding voraciously on reaching salt water.

b. *The head-to-current impulse.*

Not the least brilliant page of Romanes's *Mental Evolution in Animals* is that in which he argues that the migratory instinct of the young bird is inherited memory, and that when it is asked: Memory of what, it suffices to answer: Memory of exactly what the old bird remembers, whatever that may be. He ends by citing the belief of Mr. Black that swallows migrate

[1] Science Sketches, pp. 58-59.

against the south wind, and points out that such a habit could easily be inherited, the warm moist wind exciting an impulse to fly against it. Whatever the case may be with swallows, a strictly analogous factor appears to be the dominant one in guiding the anadromes, namely the head-to-current impulse. This was discovered as soon as fish culture came into vogue. Some of the first fish culturists being somewhat sympathetic toward their finny friends which had such long distances to travel, conceived the idea of making pools in which the fish could rest in their progress up a fishway, with the result that the fish having, so to speak, lost their guiding star, after trying in vain to find among the cross currents a predominant one, finally gave it up and headed to the vortex current floated round and round with (or rather, against) it. Also fish neglect a fishway which does not have a sufficient volume of outflow to attract their attention to its mouth, and one which, though possessing a fair volume, is disadvantageously situated (for example, near a larger outflow, or too far downstream on one side) to follow the main current to the foot of the dam. Finally this head-to-current impulse is so strong that after the migration is over and the heading to current consequently is no longer of use, the salmons still head to the current when floating down stream. It is possible that in the case of species which return to sea, this may have a protective function.[1]

Having seen what determined the beginning of the journey we may now see what determines its end. Given the salmon type of egg and the anadromous habit, natural selection must eliminate all those individuals which do not continue to follow up the ever receding suitable physical conditions (gravelly stretches), and suitable thermal conditions. These coincide only at the headwaters. It is then not necessary to imagine an "unerring instinct." All we have to imagine is a fish started on its way in obedience to one stimulus (temperature trend) recurring in its environment in the exact order in which it has, during incalculable time, recurred in the environment of its progenitors, and, later, being forwarded on its way by a second stimulus (current) which succeeds the first in the exact order in which for incalculable time it has succeeded it in the history

[1] Very recently my friend, Dr. F. Schwyzer, has drawn my attention to the following: *Electrotropismus* by Eugen Blaisius & Fritz Schwyzer (Pflüger's Archiv., 1893, vol. 53). Among other facts the authors observed that under the action of the constant current certain Cyprinids (carp, tench, and others), and the brown trout (*Salmo fario*) underwent a remarkable and fairly constant re-orientation with the head to the positive pole. Fish might be supposed to be subjected to electric stimuli arising from friction between the water and its banks. On the whole, however, the facts adduced would seem to be of a different kind from those of electrotropism.

of the race; and further to imagine the fish impelled forward by pure *vis inertiae* until checked by the interposition of a supersessory inhibitory stimulus (approaching or complete ripeness) and its simultaneous arrival at the spawning grounds. For those who have followed the preceding reasoning, not much argument will be required to show that these last two factors must (through natural selection) coincide. To those who might, for any reason of their own, still urge that this view of a fish as on a par with an automobile torpedo, is inconceivable, it may be answered that while the fish may in addition be a more or less conscious torpedo, it is not necessary to assert it to be any more than such an automobile. In saying that it is a *fish* which is migrating we say it is an organism which has, via natural selection, become *oriented parallel to its environment.* Probably few realize fully what that means. It means nothing less than that to a certain stimulus (temperature trend) it *can respond but in one way.* There is no "choice" in the matter. If there were any "choice" in past ages, and the choosers chose otherwise, they went fossil rapidly and our fish is not their descendant. Again, saying it is a *fish* means that after responding to temperature trend in the one way possible to it, it will respond to the supersessory stimulus (current) in the one way possible to it, and so on. Thus a repetend of function arises merely through a repetend of stimuli, each singly evoking appropriate response in an animal which is *the* one out of many failures and partial successes which could respond *seriatim* in just the order and to just the extent demanded as the price of its existence.[1]

c. Choice of spawning grounds.

Spawning grounds are mainly of three kinds: mud, weeds, and sand, gravel and rock. The selection is by no means a matter of chance, and though too few data exist for the tracing of every detail, certain salient facts are explicable and at least some of the factors can be indicated. These go to show that the choice of spawning grounds has been determined by the egg type via natural selection.

[1]After returning the proof I have seen the paper by Rutter in the *Popular Science Monthly* for July, 1902. It demonstrates beyond the possibility of cavil, the utterly mechanical and unintelligent nature of the phenomenon. In the ocean, fish in general, move against the various local currents produced by the tides. Thus a basis for the elaboration of the head-to-current impulse already existed, prior to the evolution of anadromy. Rutter shows that the Chinook (or Sacramento) Salmon runs into the rivers against the ebb tide. As soon as the tide turns the fish turn and run out against the flood tide. But the flood tide being of shorter duration than the ebb tide, they do not run out as far as they ran in. Consequently, day by day they ascend farther, until past the limital region where tidal movement gives place to river current.

Mud (apart from weeds). It is almost impossible that a mud bottom should be a successful spawning ground, as the eggs will almost inevitably be asphyxiated. Wherefore fishes experiencing an impulse to spawn on such bottom will leave few descendants to inherit their delicately sensitive mucous membrane, while those having an impulse to seek harder bottom will transmit to a larger progeny their more roborant mucous membrane. Further, the exception sustains the rule, the only species spawning on mud bottom being certain catfishes, the females of which excavate nests, and attend to (probably aerate) the eggs, and care for the fry.

Weeds. Here many species spawn, but they are those with adhesive eggs. In this case, too, physical conditions have determined function, for in these species the impulse to rub the genitals against the bottom is absent, the spawning being done at a leap at, or above, the surface.

Sand, gravel, and rock. The nature of these bottoms implies current or wave action sufficiently strong to habitually drive off the mud. And species with separable sinking eggs can safely deposit them here, and here only. Wherefore, given lengthening streams, those individuals will be constantly selected, which spurn the more accessible, softer bottoms, to ascend toilsomely to the current-swept stretches above.

On this class of bottoms some species build "nests" which can be traced in growing complexity. Probably mere restlessness while on the beds (which is exhibited by many species) may have formed the point of departure. This would be highly advantageous if it succeeded in covering over even only a few eggs at first, for the cover of porous sand or gravel would tend to preserve the eggs from egg eaters, and light,[1] and thereby to the predominant survival of over restless fish. The gradations in complexity of the nests favor this view.

[1] In the early days 30,000 eggs were lost from diffused daylight, and now hatching troughs are provided with light-proof covers.